

# Dependence of the Endangered Black-Capped Vireo on Sustained Cowbird Management

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**Abstract:** Conservation-reliant species depend on active management, even after surpassing recovery goals, for protection from persistent threats. Required management may include control of another species, habitat maintenance, or artificial recruitment. Sometimes, it can be difficult to determine whether sustained management is required. We used nonspatial stochastic population projection matrix simulation and a spatially explicit population model to estimate the effects of parasitism by a brood parasite, the Brown-headed Cowbird (*Molothrus ater*), on a population of endangered Black-capped Vireos (*Vireo atricapilla*). We simulated parasitism as a percentage of breeding vireo pairs experiencing decreased fecundity due to cowbirds. We estimated maximum sustainable parasitism (i.e., highest percentage of parasitized vireo breeding pairs for which population growth is  $\geq 1$ ) with the nonspatial model under multiple scenarios designed to assess sensitivity to assumptions about population growth rate, demographic effects of parasitism, and spatial distribution of parasitism. We then used the spatially explicit model to estimate cumulative probabilities of the population falling below the population recovery target of 1000 breeding pairs for a range of parasitism rates under multiple scenarios. We constructed our models from data on vireos collected on the Fort Hood Military Reservation, Texas (U.S.A.). Estimates of maximum sustainable parasitism rates ranged from 9–12% in scenarios with a low (6%) vireo population growth rate to 49–60% in scenarios with a high (24%) growth rate. Sustained parasitism above 45–85%, depending on the scenario, would likely result in the Fort Hood Vireo population dropping below its recovery goal within the next 25 years. These estimates suggest that vireos, although tolerant of low parasitism rates, are a conservation-reliant species dependent on cowbird management.

**Keywords:** conservation-reliant, HexSim, *Molothrus ater*, population model, simulation, spatially explicit, stochastic, *Vireo atricapilla*

Dependencia de *Vireo atricapilla*, Especie en Peligro, hacia el Manejo Sostenido de *Molothrus ater*

**Resumen:** Las especies dependientes de la conservación dependen del manejo activo, incluso después de obtener las metas de recuperación, para la protección de amenazas persistentes. El manejo requerido puede incluir el control de otra especie, el mantenimiento del hábitat o el reclutamiento artificial. Algunas veces puede ser difícil determinar si un manejo sostenido es requerido. Usamos una simulación de matriz de proyección de población estocástica y no espacial y un modelo de población espacialmente explícito para estimar los efectos del parasitismo por una especie parásita de reproducción, *Molothrus ater*, sobre una población de la especie en peligro *Vireo atricapilla*. Simulamos el parasitismo como un porcentaje de parejas de vireos que experimentan fertilidad baja debido a los *M. ater*. Estimamos el máximo parasitismo sostenible (p. ej.: el porcentaje más alto de parejas reproductivas parasitadas para las cuales el crecimiento poblacional es  $\geq 1$ ) con el modelo no espacial bajo escenarios múltiples asignados para estudiar la sensibilidad a los supuestos sobre la tasa de crecimiento poblacional, los efectos demográficos del parasitismo y la distribución espacial del parasitismo. Después utilizamos el modelo espacialmente explícito para estimar

las probabilidades acumulativas de que la población cayera por debajo del objetivo de recuperación de 1000 parejas reproductivas para un rango de tasas de parasitismo bajo escenarios múltiples. Construimos nuestros modelos a partir de datos de vireos colectados en la Reservación Militar Fort Hood, Texas (E.U.A.). Los estimados de la tasa de parasitismo máximo sostenible abarcaron desde 9–12% en escenarios con una tasa baja de crecimiento poblacional (6%) de vireos hasta 49–60% en escenarios con una tasa alta de crecimiento (24%). El parasitismo sostenido por encima del 45–85%, dependiendo del escenario, probablemente resultaría en la población de vireos de Fort Hood disminuyendo por debajo de su objetivo de recuperación dentro de los siguientes 25 años. Estos estimados sugieren que los vireos, aunque tolerantes a las tasas bajas de parasitismo, son una especie cuya conservación depende del manejo de *M. ater*.

**Palabras Clave:** conservación dependiente, espacialmente explícito, estocástico, HexSim, modelo de población, *Molothrus ater*, simulación, *Vireo atricapilla*

## Introduction

Recovery to the point of self-sufficiency may be unattainable for the majority of endangered species (Scott et al. 2010). Such conservation-reliant species may reach abundances greater than their prescribed recovery goals, but their risk of future population decline would be high without ongoing management and protections (Scott et al. 2005). Conservation-reliant species most often require control of other species (e.g., a competitor or parasite), active habitat management (e.g., prescribed fire), artificial recruitment (e.g., captive breeding), or control of direct human effects (e.g., hunting). Of these, control of other species is the most commonly required management action (66% of threatened and endangered species in the United States) (Scott et al. 2010).

Active control of Brown-headed Cowbird (*Molothrus ater*) populations has proven an effective management action for many songbird species. The cowbird is a brood parasite with multiple hosts (Smith 1999). Effects of cowbird parasitism on host populations are variable and most species are able to sustain low to moderate parasitism levels (Smith 1999). However, cowbirds are considered a major threat to the endangered Black-capped Vireo (*Vireo atricapilla*), the Least Bell's Vireo (*Vireo bellii pusillus*), the Kirtland's Warbler (*Dendroica kirtlandii*), and the Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (Eckrich et al. 1999; Kus 1999; Whitfield & Sogge 1999; DeCapita 2000). Aggressive cowbird trapping and shooting facilitated population increases in all 4 species and has since been adopted to support songbird populations elsewhere. Despite this success, cowbird trapping and euthanasia remains controversial because cowbirds are a native North American grassland species whose past range expansion was a response to anthropogenic land-use changes (Smith 1999). Furthermore, cowbird trapping does not permanently reduce cowbird population densities and may be required annually at high cost (DeCapita 2000). And although trapping may provide a short-term reprieve for host species, it does not address the underlying causes of cowbird range expansion (Hall & Rothstein 1999). Alternative management actions, such as restoring host nesting habitat (Hall

& Rothstein 1999; DeCapita 2000) and decreasing or moving cattle during songbird nesting seasons (Goguen & Mathews 2001; Kostecke et al. 2003) may prove to be more effective long-term solutions for host species conservation.

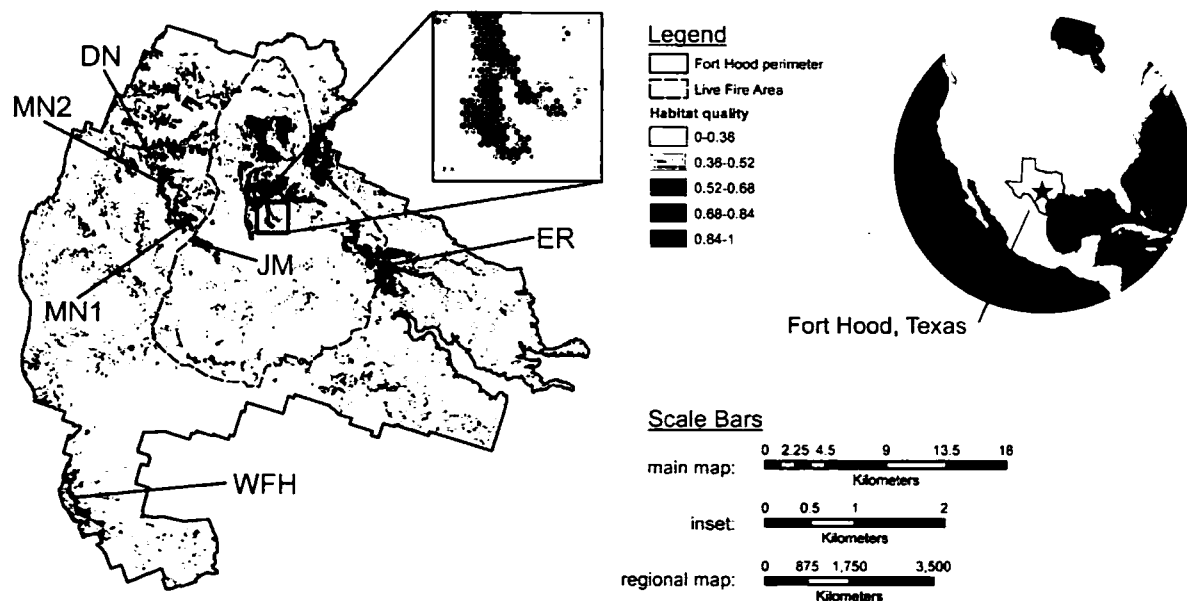
We identified the Black-capped Vireo's maximum sustainable level of brood parasitism with stochastic simulation. We estimated maximum sustainable parasitism under multiple scenarios designed to assess model sensitivity to assumptions about population growth rate and the spatial distribution and demographic effects of parasitism. We then used a spatially explicit individual-based population model to estimate cumulative probabilities of the population falling below the population recovery target of 1000 breeding pairs for a range of parasitism rates. Both models were parameterized with long-term demographic data from the Fort Hood Military Reservation, Texas (U.S.A.), and the spatial model was run on a high-resolution vireo habitat-suitability map for Fort Hood derived from remotely sensed data on vegetation structure and composition.

## Methods

### Study Area and Species

Fort Hood, an 87,890-ha military installation in north-central Texas (97°44'W, 31°12'N) (Fig. 1), supports the largest known population of Black-capped Vireos in the United States and is managed by one agency (Cimprich & Kostecke 2006). Fort Hood is located at the intersection of the Edwards Plateau and the Cross Timbers and Southern Tallgrass Prairie ecoregions. Vegetation is composed of woodlands and upland forest (47%), grasslands (34%), and shrubland and riparian forest (4% and 3%, respectively).

The Black-capped Vireo is a Nearctic Neotropical migrant passerine that breeds in north central Mexico, Texas, and central Oklahoma (U.S.A.) and winters along Mexico's Pacific slope (Graber 1961). The vireo was listed in 1987 as endangered under the U.S. Endangered Species Act (Ratzlaff 1987) and is currently classified as



**Figure 1.** Map of Black-Capped Vireo habitat quality (0, lowest; 1, highest) on the Fort Hood Military Reservation in Texas (U.S.A.). Habitat quality scores are based on an empirical habitat suitability model incorporating measures of vegetation type and structure and soil depth (Wilsey et al. 2012). Inset shows a portion of the hexagonal grid of habitat quality used in the spatially explicit population model. Letter codes identify locations of 6 demographic study areas for which names and extents are listed in Table 2.

vulnerable by the International Union for Conservation of Nature (BirdLife International 2012). Threats to the vireo include brood parasitism by cowbirds, rangeland expansion, forest succession, and urbanization (Tazik et al. 1993; Wilkins et al. 2006).

The Brown-headed Cowbird is a Nearctic migrant passerine that breeds in north central Mexico, throughout the United States and southern Canada, and in the northern prairie region of Canada (Lowther 1993). On Fort Hood, cowbirds parasitize the nests of multiple hosts, including Black-capped Vireos, White-eyed Vireos (*Vireo griseus*), Northern Cardinals (*Cardinalis cardinalis*), and Painted Buntings (*Passerina ciris*) (Barber & Martin 1997).

On Fort Hood, Black-capped Vireo abundance has increased from hundreds to thousands since 1987, when an extensive cowbird control program incorporating both trapping in cowbird foraging habitats and shooting in vireo breeding habitats began (Eckrich et al. 1999). Current estimates of vireo populations on Fort Hood have exceeded recovery goals (USFWS 2005; Wilkins et al. 2006), but it is unclear whether vireo recovery is self-sustaining or dependent on cowbird control programs.

#### Estimating Maximum Sustainable Parasitism

We used nonspatial stochastic projection matrix simulation (Morris & Doak 2002) to estimate the maximum sustainable parasitism rate of the Fort Hood vireo popula-

tion by simulating parasitism as a proportional decrease in fertility. We defined maximum sustainable parasitism as the highest rate at which the estimated population growth rate ( $\lambda$ ) is greater than or equal to 1. We used the following equation to estimate stochastic growth:

$$e^{\left( \frac{\sum_{t=0}^n \ln \left( \frac{N_{t+1}}{N_t} \right)}{n} \right)},$$

where  $N_t$  is the simulated population abundance at time  $t$  and  $n$  is the number of simulation years. Stochastic simulations were based on a 2-stage projection matrix (i.e., Leslie matrix) applied as a birth-pulse, prebreeding census model with parameters for each annual projection matrix drawn from their respective distributions (stretched beta and beta distributions for fecundity and survival parameters, respectively) (see "Model Scenarios and Analyses" for parameter values). We simulated 100,000 years with 500 random matrices and estimated the stochastic growth rate ( $\lambda$ ) and 95% confidence interval (Morris & Doak 2002). We then used the less computationally efficient spatially explicit population model to examine the effects of parasitism on vireo abundance on Fort Hood.

#### Estimating Vireo Abundance

We used a spatially explicit population model to estimate cumulative probabilities of the vireo population falling below its target recovery abundance under increasing parasitism. We built the population model

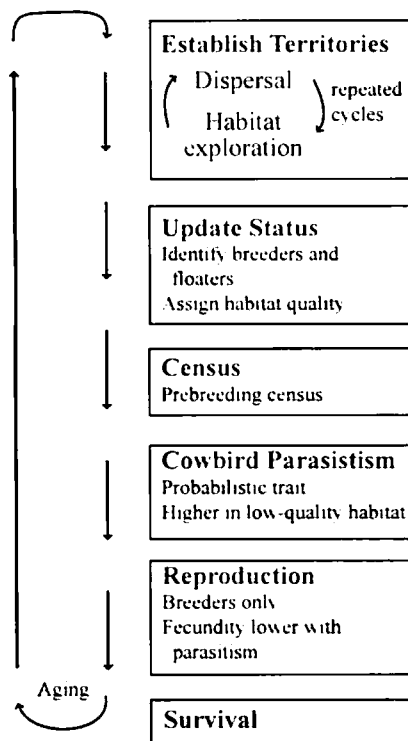


Figure 2. Events included in a spatially explicit population model of Black-Capped Vireo constructed in the HexSim (Heinrichs et al. 2010) modeling platform.

with the HexSim modeling platform (Heinrichs et al. 2010), an updated version of the PATCH population model (Schumaker et al. 2004). The vireo model is a stochastic stage-based projection matrix model based on birth-pulse, prebreeding census data. The model simulates annual life-history events, including dispersal and territory establishment, reproduction, survival, and cowbird parasitism (Fig. 2). The 2-stage model has an annual time step and incorporates environmental stochasticity into annual reproduction and survival rates. We built a male-only model because all count data for Fort Hood refers to male vireos and fecundity estimates are per male territory (Cimprich & Heimbuch 2012). Parameter values were based on published estimates when available and unpublished monitoring data from The Nature Conservancy of Texas' Fort Hood Project (TNC-FHP).

HexSim is a standalone spatial modeling platform that can import shapefile and raster data. Spatial inputs to HexSim are mapped to hexagon grids, rather than square-celled grids, to standardize between-cell distances. Vireo habitat availability and quality on Fort Hood was based on an empirical habitat suitability model (Wilsey et al. 2012). This model was built with data from vireo surveys conducted in 2002–2003 (Cimprich & Kostecke 2006) and maps of vegetation type, soil depth, and lidar-derived vegetation heights and edge-density estimates. Model ac-

curacy was 76% for predicting presences and absences in a subset of points held out of the data set used to build the model (Wilsey et al. 2012). We used the probability of vireo presence as a continuous measure of habitat quality. Habitat quality was mapped to a hexagonal grid with a resolution of 0.56 ha/hexagon (Fig. 1). This resolution was selected to best approximate observed vireo densities while minimizing simulation run time.

Each time step begins with a movement event in which individuals disperse and attempt to establish territories with sufficient resources (Fig. 2). This is accomplished through repeated cycles of dispersal and exploration. Beginning from an individual's hexagon location the previous year (or a random location during model initialization), dispersal distances are selected from a lognormal distribution ( $\mu = 1.0$  km,  $\sigma = 0.8$  km). Dispersal is simulated with a Markov Chain model with spatially autocorrelated movement and attraction to high-quality habitats. Parameters for the lognormal distribution and maximum number of cycles were set such that the mean and median simulated distance traveled per individual (summed across repeated dispersal cycles) closely approximated the mean and median dispersal distance (2.8 and 1.4 km, respectively) of approximately 200 dispersal events observed through mark-recapture and resighting of individuals on Fort Hood (unpublished data, TNC-FHP). Ninety-five percent of simulated dispersal events were <15 km. Following dispersal, individuals explore hexagons at their new location and only attempt to disperse again if they do not find sufficient resources. Available resources in each hexagon are equivalent to that hexagon's habitat quality score. Individuals unable to establish a territory after 35 attempts become nonbreeding floaters. Habitat saturation and the inability of some individuals to establish territories and reproduce introduce density-dependent limits on population growth. We based the target resource requirements (minimum and maximum) for territories on density estimates from intensive monitoring in 6 demographic study areas (Fig. 1; Cimprich & Heimbuch 2012). Resulting territories are 2 hexagons (1.12 ha) in size and larger, depending on habitat quality. Following the movement event, individuals are identified as either breeders or floaters and their territories are classified as located in either high- or low-quality habitat based on their locations. High-quality hexagons were those in which the median habitat quality in a  $5 \times 5$  cell ( $\sim 14$  ha) moving window was above 0.68 (the midpoint of habitat quality scores among grid cells classified as habitat). Finally, a prebreeding population census was completed.

We simulated environmental stochasticity by having HexSim step through 100 sets of 50 stochastic projection matrices for 100, 50-year simulations. We created the projection matrices by first selecting 100 sets of 50 values from a standard normal distribution. We repeated this for fecundity and juvenile and adult survival. We then used these random deviates to generate 100 sets of 50

Table 1. Values for key parameters in the scenarios tested with the HexSim vireo population model.

Scenario	Fecundity <sup>a</sup> ( $\mu$ , $\sigma$ )	Juvenile survival ( $\mu$ , $\sigma^b$ )	Adult survival ( $\mu$ , $\sigma^b$ )	Lambda ( $\lambda$ )
Empirical <sup>c</sup>	1.92, 0.58	0.42, 0	0.50 <sup>d</sup> , 0.07	0.92
Population growth				
Low	2.4, 0.58	0.40, 0.07 <sup>e</sup>	0.62, 0.07	1.06
Moderate	2.4, 0.58	0.52, 0.07	0.62, 0.07	1.14
High	2.5, 0.58	0.57, 0.07	0.69, 0.07	1.24

<sup>a</sup>Fledglings per male territory.

<sup>b</sup>Model-based estimate of process error (Kostecke & Cimprich 2008).

<sup>c</sup>Estimates derived from intensive nest monitoring and mark-recapture monitoring in the demographic study areas (Fig. 2).

<sup>d</sup>Mean estimate of adult survival from 1997–2006 (Kostecke & Cimprich 2008).

<sup>e</sup>We replaced the estimate of zero process error for juvenile survival with the process error estimate for adult survival (Supporting Information).

fecundity and survival matrices by converting the random normal deviates into stretched beta (for fecundity) and beta distributions (for survival, Morris & Doak 2002). Mean and standard deviation estimates for fecundity were based on observed fledging counts in demographic study areas from years with <10% observed nest parasitism (Supporting Information). Values for postfledgling juvenile survival and adult survival were derived from model-based estimates derived from mark-recapture data (Supporting Information). Parameter values varied among scenarios (described below and summarized in Table 1). The model-based estimate of environmental variability (i.e., process error) for juvenile survival was zero (Supporting Information), so we substituted the estimate for adult survival (Table 1). Generating all of our fecundity and survival matrices from the same 100 sets of 50 random deviates helped isolate the effect of modeled scenarios from the variability due to simulated environmental stochasticity in general. We ran 100, 50-year simulations for each scenario (described below) with each run proceeded by 10 simulation years run with vital rates consistent with a stationary population and no environmental stochasticity. This 10-year model-initialization period allowed simulated individuals to colonize habitats throughout the simulation landscape and to reach a total population size (simulated median = 5218) consistent with the current population estimate of 5408 breeding males (Cimprich & Heimbuch 2012).

### Model Scenarios and Analyses

We based our estimates of vireo vital rates on a 9-year mark-recapture study (Kostecke & Cimprich 2008) and 8 years of intensive nest monitoring (Cimprich & Heimbuch 2012) conducted on Fort Hood (Supporting Information). The population growth rate for a 2-stage vireo population projection matrix (i.e., Leslie matrix) parameterized with empirical estimates of fecundity and juvenile and adult survival from these studies (Table 1) is declining ( $\lambda = 0.92$ ) even in the absence of cowbird parasitism. Yet, because cowbird management began in 1987, the vireo population has grown from 143 observed breeding males in 1989 (Tazik et al. 1993) to a distance-sampling

estimated 5408 breeding pairs in 2012 (Cimprich & Heimbuch 2012). Therefore, we know that empirical estimates are incorrect. Survival estimates, in particular, are likely biased low (Kostecke & Cimprich 2008) due to incomplete site fidelity (Cilimburg et al. 2002). Historical estimates of fecundity (Tazik et al. 1993) were also higher. We therefore adjusted empirical fecundity and adult survival rates to the upper limit of their 95% confidence intervals (Supporting Information). We selected the upper 95% confidence limit to remain consistent with the original empirical data. For juvenile survival, estimated standard errors were high (0.13), so we set juvenile survival at 64% of adult survival in a low-growth scenario and at 84% of adult survival in an intermediate-growth scenario. These proportions were derived from 2 model-based estimates of juvenile survival (Supporting Information), which were both well supported by data ( $\Delta\text{QAIC}_c < 2$ ) from Fort Hood (Kostecke & Cimprich 2008). Adjusted fecundity estimates were below reported estimates of maximum fecundity (Tazik et al. 1993); similar juvenile survival rates have been reported previously (Grzybowski 2005); and adult survival estimates were within reported ranges for the Black-capped Vireo (Grzybowski 1995; Weinberg et al. 1998) and White-eyed Vireo (DeSante & Kaschube 2006), a similarly-sized congener. We considered these 2 parameter sets as representative of low-growth ( $\lambda = 1.06$ ) and moderate-growth ( $\lambda = 1.14$ ) populations (Table 1).

We then generated vital rates for a high-growth ( $\lambda = 1.24$ ) scenario designed to capture the maximum potential growth rate of the Fort Hood vireo population based on past population estimates. Looking back, we have the highest confidence in the 1989 population estimate of 143 breeding males made just after the species was listed as endangered in 1987 and when vireo abundance was small and sampling effort high (Tazik et al. 1993). As the population grew in response to cowbird trapping and shooting, sampling effort did not grow commensurately and population estimates from the 1990s are generally considered less reliable and biased low. No total abundance estimates were made from 1997–2004. Recent efforts, including the use of a habitat model based on remote-sensing data (Wilsey et al. 2012) and access to

the Live Fire Area in 2012 for density surveys, make the 2012 total vireo population estimate the most reliable. We used the 2012 estimate, 5408 breeding pairs (Cimprich & Heimbuch 2012), as an estimate of Fort Hood's carrying capacity. Density surveys suggest that the vireo population was stable a number of years previous to 2012. Population growth was observed in burned habitats as late as 2004 (Cimprich 2004) and density estimates peaked in 2006 (Cimprich 2006). We therefore estimated that Fort Hood reached its carrying capacity of 5408 breeding pairs in 2006. Growth from 143 breeding pairs in 1989 to 5408 in 2006 corresponds with the 2.4% geometric growth of the high-growth scenario.

We parameterized the high-growth model through stochastic projection matrix simulation. First, we identified plausible ranges for each of the 3 parameters: fecundity, juvenile survival, and adult survival. Minimums were set to empirical means (Supporting Information) and maximums were drawn from the literature or from maximum values recorded on Fort Hood. We then generated 28,980 parameter sets and estimated their stochastic growth rates, keeping only those parameter sets for which  $\lambda = 1.24$  fell within the simulated 95% confidence interval.

In addition to population growth rates, we considered the effects of habitat-dependent parasitism rates and nonzero fecundity of vireos experiencing nest parasitism. Nest parasitism rates are ~10% higher in low-quality habitats created by military training activities (Noa et al. 2007). We therefore simulated 10% higher parasitism in low-quality habitats. Finally, we included a scenario in which the fecundity of vireos with parasitized nests was 17% of vireos with nonparasitized nests (Tazik et al. 1993), even though parasitized nests rarely fledge vireos (Pease & Grzybowski 1995), and since 2002 have done so on Fort Hood only when the cowbird egg fails to hatch.

We used nonspatial stochastic projection matrix simulation to estimate the maximum sustainable parasitism rate for each scenario. For the high-growth scenario, we initially selected 3 parameterizations (one with relatively high fecundity, one with high-adult survival, and one balanced scenario with mid-range values for fecundity and survival), but estimates of maximum sustainable parasitism were within 2 percentage points of one another, so we opted to only report on the balanced scenario for simplicity. Simulations were run for the 3 growth scenarios alone and in combination with scenarios for habitat-dependent parasitism and nonzero fecundity with parasitism for a total of 9 scenarios: low growth, moderate growth, high growth, low-growth habitat-dependent parasitism, moderate-growth habitat-dependent parasitism, high-growth habitat-dependent parasitism, low-growth nonzero fecundity with parasitism, moderate-growth nonzero fecundity with parasitism, and high-growth nonzero fecun-

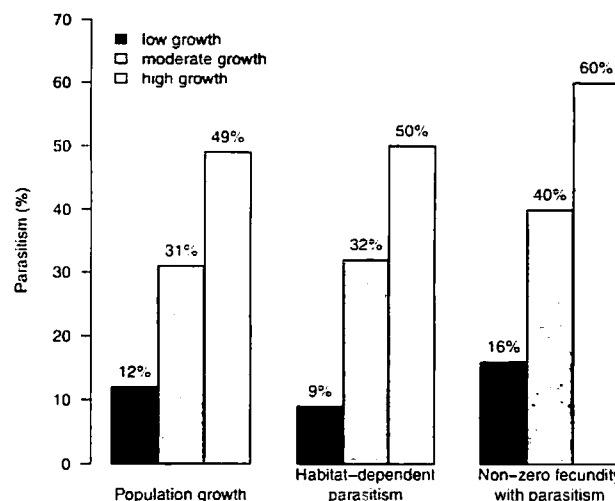


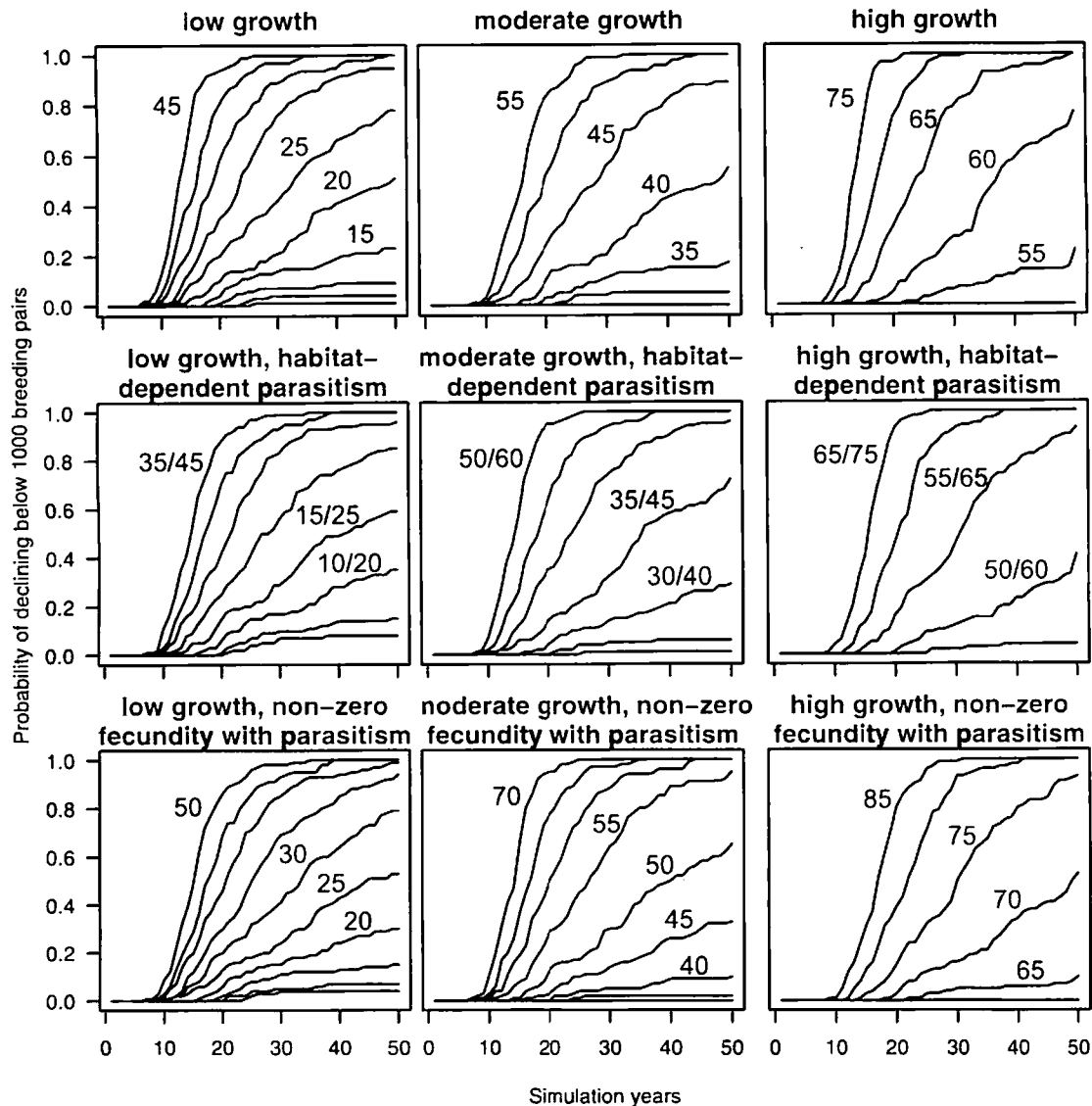
Figure 3. Estimated maximum sustainable parasitism rate for the low-growth ( $\lambda = 1.06$ ), moderate-growth ( $\lambda = 1.14$ ), and high-growth ( $\lambda = 1.24$ ) Black-capped Vireo population scenarios (derived from stochastic population projection matrix simulation).

dity with parasitism. For each scenario, we estimated  $\lambda$  for all parasitism rates (1–100). In this analysis, we simulated habitat-dependent parasitism as an area-weighted average of rates in high- and low-quality habitats and nonzero fecundity with parasitism by adding parasitized fecundity to nonparasitized fecundity.

We then used the spatially explicit population model to estimate the probability of the Fort Hood population falling below the recovery goal of 1000 breeding males under increasing parasitism. We generated cumulative probability distributions based on the 100, 50-year simulations for a range of parasitism rates simulated at 5% intervals.

## Results

Vireo populations on Fort Hood tolerated low to moderate (12–49%) levels of sustained parasitism based on our low-, moderate-, and high-growth scenarios (Fig. 3). In general, estimated maximum sustainable parasitism rates were approximately double the stochastic growth rate expressed as a percent. For example, the low-growth scenario represented a 6% growth rate and sustained a maximum 12% parasitism rate. Area-weighted habitat-dependent parasitism simulated generally the same relation as the nonhabitat-dependent scenarios. Finally, increasing the fecundity of parasitized territories to 17% of nonparasitized fecundity increased maximum sustainable parasitism by 4%, 9%, and 11% in the low-, moderate-, and high-growth scenarios, resulting in maximum sustainable parasitism rates > 2.5 times the stochastic growth rate.



**Figure 4.** Cumulative probability of the Fort Hood Black-capped Vireo population dropping below 1000 breeding pairs under 9 scenarios that address assumptions about population growth rate (top row), spatial distribution of parasitism (middle row), and demographic effects of parasitism (bottom row). Probability distributions are based on 100, 50-year simulations with a spatially explicit population model. Lines show the cumulative probability distribution for multiple parasitism rates separated by 5% intervals. Numbers next to lines identify simulated parasitism rates. Rates in high- and low-quality (high/low) habitats are included for the habitat-dependent parasitism scenarios.

We also estimated the probability that increased parasitism would cause the vireo population to fall below the target of 1000 breeding pairs in the next 25–50 years (Fig. 4). Parasitism rates leading to rapid population declines were necessarily higher than estimated maximum sustainable parasitism rates. A sustained parasitism rate of 45% caused more than 95% of simulated populations in the low-growth scenario to fall below 1000 breeding pairs within at least 25 years. The same outcome required sustained parasitism rates of 55% and 75% in the

moderate- and high-growth scenarios. A similar pattern occurred for the habitat-dependent parasitism scenarios, but with increased sensitivity to parasitism in high-quality habitats. Sustained parasitism of 50%, 70%, and 85% was required to drop 95% of simulated populations in the low growth, moderate growth, and high growth with nonzero fecundity with parasitism scenarios below the recovery target.

Simulated vireo densities in 5 of the 6 demographic study areas ranged from 10% less to 31% more than

Table 2. Observed and simulated vireo densities in demographic study areas.

Study area (abbreviation) <sup>a</sup>	Area (ha)	Max. density (2005–2010)	Mean simulated <sup>b</sup> density (95% CI)
Donut habitat (DN)	95.3	0.26	0.34 (0.33–0.35)
East range (ER)	88.4	0.67	0.69 (0.67–0.74)
Manning 1 (MN1)	23.3	0.65	0.69 (0.69–0.73)
Manning 2 (MN2)	46.3	0.78	0.84 (0.81–0.88)
West Fort Hood (WFH)	103.3	0.42	0.38 (0.35–0.44)
Jack Mountain (JM)	79.7	0.37 <sup>c</sup>	0.82 (0.80–0.85)

<sup>a</sup>Study area abbreviations apply to Fig. 1.

<sup>b</sup>Mean simulated densities estimated from a stationary population scenario ( $\lambda = 1.0$ ) with no parasitism in which fecundity = 2.4 fledglings per male territory, juvenile survival = 0.4, and adult survival = 0.55.

<sup>c</sup>Jack Mountain was in the Live Fire Area with limited survey access resulting in lower than expected maximum density estimates.

the maximum observed densities (Table 2). The greatest sources of error were in low-quality sites, such as Donut habitat and West Fort Hood, where birds were consistently found but occurred at lower densities than in high-quality shrubland sites. Access to the sixth study area (Jack Mountain) was restricted by its location in the Live Fire Area, a region in the center of Fort Hood where live ammunition is used. Therefore, field estimates of vireo density at the Jack Mountain study area were likely biased low.

## Discussion

Rising parasitism rates have the potential to reverse vireo population recovery on Fort Hood. Our results suggest that the Fort Hood vireo population can tolerate parasitism levels below 9–16% with a high degree of confidence but that fewer than 1000 breeding pairs—the current recovery goal for Fort Hood (USFWS 2005) based on the estimated minimum viable population (USFWS 1996)—could remain over 25 years if parasitism rates climb above 45–85%, depending on the scenario. Given that nest parasitism rates as high as 90% have been documented on Fort Hood (Tazik et al. 1993), our results suggest the vireo is conservation reliant (Scott et al. 2005) and that any reduction in protection status should include active cowbird management.

The vireo's maximum sustainable parasitism rate was estimated previously as 42% and 55% by 2 different methods (Tazik et al. 1993). Vital rates were comparable to our moderate-growth scenario, but estimates of the parasitism effects were based on simulations of nesting outcomes parameterized with daily probabilities of nest survival (42%) and an empirical linear model relating fecundity to parasitism rate (55%). Our estimates of maximum sustainable parasitism under the moderate-growth scenario (31–40%) were lower. Because demographic rates were nearly the same, differences likely reflect their parameterization of the daily nest survival model and linear model. We consider ours to be updated results given that our estimates were based on several more years of monitoring data collected with improved methods. Our

inclusion of estimates of environmental stochasticity may also have contributed to the difference in results. The U.S. Fish and Wildlife Service vireo population viability analysis did not identify a maximum sustainable parasitism rate, per se, but did identify minimum fecundity rates required to maintain a stable population across a range of parasitism rates (USFWS 1996). They concluded that 2.5 fledglings/female were required to maintain the probability of population extinction within 100 years below 5%. Our estimates of juvenile and adult survival were higher, confounding any direct comparison. However, results from our high-growth scenario suggested that population decline could result if parasitism rates climb above 49% even if fecundity is 2.5 (Table 1 & Fig. 3). Parasitism rates as high as 90% have been documented on Fort Hood (Tazik et al. 1993) and are theoretically plausible (Pease & Grzybowski 1995). Therefore, vireo declines would likely result from cessation of cowbird trapping under any of our modeled scenarios.

Other factors, not included in our model, may further reduce population growth rates if cowbird parasitism is allowed to increase. Controlling cowbird populations may also reduce nest predation. Cowbirds, along with snakes, are common vireo nest predators (Stake & Cimprich 2003; Conkling et al. 2012). Predation may create additional cowbird parasitism opportunities when vireos re-nest (Hoover & Robinson 2007). Observations of increased predation risk later in the breeding season on Fort Hood and low depredation rates in parasitized nests are consistent with this hypothesis (Conkling et al. 2012). Therefore, any reduction of cowbird controls may lead to higher vireo nest predation and lower fecundity. Cowbird parasitism rates are also known to vary annually (Smith et al. 2012) and with host densities (Barber & Martin 1997). Including environmental stochasticity in parasitism rates would likely increase the overall tolerance of the population to parasitism. Improved understanding of cowbird population dynamics and preferences for breeding habitat on Fort Hood may also increase spatial variability in parasitism rates and identify vireo refugia. Finally, second-year birds have demonstrated lower rates of fecundity (Weinberg et al. 1998), but this was not included in our model. Second-year birds often nest later



and may experience higher parasitism rates. This would likely lower the maximum sustainable parasitism rate.

### Model Uncertainty

We addressed uncertainty by calculating model outputs under multiple scenarios. Our low- and moderate-growth scenarios were based on empirical estimates of fecundity and survival and the high-growth scenario was parameterized based on population-abundance data. Both sources are justifiable on their own, and together they provide reasonable bounds on the vireo's population growth rate with cowbird trapping. Of the scenarios, the 24% growth rate was the most remarkable. Mapped territories were generally larger and observed fecundity higher (Tazik et al. 1993; Weinberg et al. 1998) in the 1990s than the 2000s, suggesting that population growth rates in the initial years of cowbird control were higher than today. Immigration could also explain the rapid growth of the Fort Hood population. However, habitats in the surrounding area are limited in extent and located on private lands with no cowbird trapping. Therefore, immigration is likely low. Ongoing nest monitoring and mark-recapture studies in habitat patches surrounding Fort Hood initially support the assumption that Fort Hood serves as a source population for the region (L. Walker, personal communication). In this analysis, we modeled Fort Hood as a closed population, but the high-juvenile recruitment in the high-growth scenario could also be viewed as an estimate of apparent survival incorporating immigration (Abadi et al. 2010). Finally, vireos today occupy many habitats on Fort Hood that were not considered habitat in 1989, suggesting that brood parasitism, not habitat availability, limited vireo population growth historically.

Increasing the fecundity of parasitized breeding pairs decreased the vireo's overall sensitivity to simulated parasitism. The Black-capped Vireo is small and therefore more affected by parasitism than other hosts (Grzybowski 1995). The similarly sized Warbling Vireo (*Vireo gilvus*) also fails to produce young when parasitized (Ward & Smith 2000). Tazik et al. (1993) reported nonzero fecundity of vireos with parasitized nests, but this occurred when cowbird eggs failed to hatch. Cases of vireos fledging both vireo and cowbird young are currently rare on Fort Hood (one record since 2002) and have been considered rare elsewhere (Pease & Grzybowski 1995). Renesting can also increase fecundity of breeding pairs that are parasitized on their first nesting attempt, but is rare. Fecundity of parasitized vireos is likely closer to zero than the 17% modeled in the nonzero fecundity with parasitism scenario.

Finally, simulated densities in the demographic study areas were generally higher than observed (Table 2); the greatest errors occurred at low-quality sites. Therefore, the habitat model (Wilsey et al. 2012) used did not fully resolve differences in habitat quality among occupied

sites and led to less-accurate estimates of abundance. A higher resolution habitat model or model predicting vireo density may improve model fit and increase probabilities of the vireo population falling below 1000 breeding pairs at lower parasitism rates.

### Implications of Conservation Reliance

We conclude that the Fort Hood Black-capped Vireo population is likely conservation reliant (Scott et al. 2005). Sustained parasitism rates as low as 45% could result in the vireo abundances falling below the minimum viable population target within 25 years. Thus, to ensure that vireo populations are maintained, plans for sustained cowbird management will need to be a prerequisite for any change in the protection status of the vireo across its range. Few alternatives exist to cowbird trapping and shooting. Reduced cattle stocking rates may lower cowbird abundances and vireo parasitism. However, a short-term study on Fort Hood suggested that effects would only be significant if stocking adjustments included both Fort Hood and surrounding rangelands (Kostecke et al. 2003), and this may be politically infeasible.

Our results suggest that Black-capped Vireo populations may be at risk wherever cowbird parasitism rates rise above 9–60%. In 2006, cowbird trapping occurred in more than half of all Texas counties with vireos and in one location in Oklahoma (Wilkins et al. 2006). If ongoing land-use change is facilitating an increase in cowbird densities, as some evidence suggests (Wilkins et al. 2006; Kostecke 2008), cowbird trapping may need to expand.

Designation as a conservation-reliant species does not necessarily preclude a reduction in a species' protected status, although it does present additional constraints (Goble 2009). Our results suggest that the successful recovery of the Black-capped Vireo will require that monitoring and control of cowbird populations, either directly or through restrictions on land use, be a precondition for a reduction in protected status.

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## Supporting Information

Estimates of vital rates for the study population of Black-capped Vireos (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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